



Effects of chronically elevated nitrogen and sulfur deposition on sugar maple saplings: Nutrition, growth and physiology

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ABSTRACT

At the Bear Brook Watershed in Maine (BBWM), we examined the effects of long-term experimentally elevated N and S deposition on foliar chemistry, growth, and photosynthetic capacity of sugar maple (*Acer saccharum*) saplings. The BBWM is a paired watershed system; one watershed has been acidified bimonthly with granular ammonium sulfate ((NH₄)₂SO₄) since 1989. The adjacent watershed is used as a reference. We observed a 56% increase in foliar Al and a 25% reduction in foliar Ca for sugar maple saplings on the treated watershed compared to reference. Foliar N (+15%), P (+10%), and K (+15%) were significantly elevated in treated saplings. Along with changes in foliar nutrients, there were significant differences in photosynthetic capacity.

Photosynthetic capacity might have been affected by foliar nutrient imbalances induced by N and S deposition, though light-saturated net photosynthesis and sapling growth were not correlated with differences in foliar nutrient content. Sapling stratum growth and allocation appeared to be determined primarily by disturbances in the overstory canopy that enhanced light conditions in the sapling stratum. Photosynthetic capacity also appeared to be closely linked to sapling density which altered light environment at the leaf-level and increased foliar temperatures. In addition, lower carboxylation capacity was related to low Ca and high Al. Electron transport efficiency and triose-phosphate utilization appear negatively influenced by increased foliar Mn, Fe, and Zn content, although the levels found in this study are below those that provide obvious symptoms of toxicity.

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1. Introduction

Sugar maple (*Acer saccharum* Marsh.) is a ubiquitous shade-tolerant species that occupies a broad niche in the deciduous forests of the northeastern U.S. and eastern provinces of Canada. It is the most abundant hardwood in New York and Vermont, and the second most abundant in Maine and New Hampshire (Lovett, 2004). The natural range of sugar maple covers areas with some of the highest N deposition rates in the eastern U.S., and sugar maple decline in some areas has been attributed, at least in part, to foliar nutrient imbalances commonly associated with high rates of acidic deposition (Kolb and McCormick, 1993; Moore et al., 2000; Duchesne et al., 2002; Schaberg, 2006). Though sulfur (S) emissions

have declined in most regions of the U.S. since the Clean Air Act of 1990, nitrogen (N) deposition in the U.S. has increased (Fenn et al., 2003; Lehmann et al., 2005; NADP, 2002–2006). Also S deposition in some U.S. areas remains high, especially in high elevation areas downwind of heavy industrialization and urbanization (Driscoll et al., 2001).

Higher nitrogen availability can sometimes stimulate growth in N limited environments (Molden et al., 2006), however N is now considered enriched in many once N-limited northern forests because of heavy inputs of N deposition (Aber et al., 1989, 2003; Matson et al., 2002; Manning, 2006). Declines in base cations (especially Ca) in many northeastern soils have been attributed to the effect of acidification of N and S deposition (Fernandez et al., 1999; Driscoll et al., 2001; Gbondo-Tugbawa and Driscoll, 2003; Bailey et al., 2003; Lawrence et al., 1999; Federer et al., 1989; Likens et al., 1998; Schaberg et al., 2001; Watmough et al., 2005). Calcium is considered an essential mineral nutrient for trees and is particularly important to sugar maple nutrition (Schaberg et al., 2001; Horsley et al., 2002). Schaberg (2006) showed a significant

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relationship between low foliar Ca (<5000 ppm) and low membrane associated Ca, which is essential for tree stress response and growth. Resupplying base cations and neutralizing acidity in sugar maple stands promotes diameter growth and increases protein production (Liu et al., 1994). A significant reduction in Ca can lead to reduction in cambial growth and sapwood area and can lead to a reduction in crown density (Shortle and Smith, 1988). Low leaf Ca and Mg has also been associated with lower photosynthetic capacity and rates (Liu et al., 1997; Elvir et al., 2006).

Nutrient availability is also an important factor for the success of sugar maple seedlings (Catovsky and Bazzaz, 2002). In the understory, sugar maple seedlings have to compete for light, rooting space, nutrients, and water. High light has been shown to make nutrient poor conditions more stressful for seedlings (Canham et al., 1996). St Clair and Lynch (2005a) found that Ca and phosphorus (P) limitations were responsible for inhibition of growth of seedlings. Additions of Ca in acidified areas have increased sugar maple seedling regeneration and vigor (Juice et al., 2006).

Bear Brook Watershed in Maine (BBWM) is the site of a long-term watershed acidification experiment designed to understand the effects of elevated N and S deposition on ecosystem processes. The treatment has resulted in the depletion of base cations from soil cation exchange sites (Fernandez et al., 2003), acceleration of N cycling (Jefts et al., 2004), and increases in N export to surface waters (Kahl et al., 1999; Fernandez et al., 2003). Mature sugar maple trees at BBWM have responded to the treatment with increased foliar N concentrations (White et al., 1999; Elvir et al., 2005), an initial increase followed by a decline in radial growth (Elvir et al., 2003), and elevated photosynthetic rates (Elvir et al., 2006).

In 2006, we investigated the effects of elevated N and S deposition on growth, foliar nutrients and photosynthetic capacity of sugar maple saplings at BBWM. We hypothesized that the treatment would lead to elevated levels of foliar N, declines in foliar base cations, and that these changes would affect their photosynthetic capacity and growth.

2. Methods

2.1. Site description

This study was conducted in 2006 at BBWM, the site of a long-term, whole-watershed experimental acidification study. The study is a paired watershed design begun in 1989 with West Bear (WB) (10.3 ha) experimentally acidified and the adjacent East Bear (EB) (11.0 ha) used as a reference. Ambient deposition (wet + dry) at BBWM was estimated at $8.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $14.4 \text{ kg S ha}^{-1} \text{ yr}^{-1}$ at the beginning of the experiment (Wang and Fernandez, 1999). Treatment on WB consists of bimonthly aerial applications of granular ammonium sulfate ($(\text{NH}_4)_2\text{SO}_4$) at $25.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $28.8 \text{ kg S ha}^{-1} \text{ yr}^{-1}$. Additional site characteristics and details of the long-term experiment have been described by Norton et al. (1999).

BBWM is located on the southeast slope of Lead Mountain (elev. 475 m) in eastern Maine ($44^\circ 52' \text{N}$, $68^\circ 06' \text{W}$), 60 km from the Gulf of Maine. The watersheds were selected based on similar slope, soils, and forest cover and were subject to two years of hydrological calibration prior to the onset of treatments (Uddameri et al., 1995). Both watersheds have first order streams which were shown to have nearly identical chemistry before treatment (Kahl et al., 1999; Norton et al., 1999). Soils are thin and vary from 0 to 1.5 m, averaging 1 m in depth. Soils are young, mostly coarse to fine loamy Haplorthods in the Tunbridge and Rawsonville developed in glacial till (Rustad et al., 1993). Climate is continental with short, warm summers. Annual precipitation has been 1.4 m on average, evenly distributed throughout the year, and average annual temperature has been 4.9°C (Fernandez et al., 2003).

The forest cover is softwood on the upper slopes with second growth northern hardwood and mixedwood forest on the mid- and lower slopes. Logging occurred in the hardwood stands prior to 1945. Dominant tree species includes red spruce (*Picea rubens* Sarg.), American beech (*Fagus grandifolia* Ehrh.), sugar maple (*A. saccharum* Marsh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britt.). Sugar maple is the third most abundant mature tree species across both watersheds, after red spruce and American beech, making up 15% of tree biomass, and 15% and 18% of mature trees per hectare on untreated EB and treated WB, respectively (Elvir, 2001).

2.2. Plots and sapling surveys

The objective of this study was to compare treated (WB) and untreated (EB) saplings that had sufficient light for potentially active growth. Sugar maple saplings were defined as individuals between 2 and 4 m in height and 0.5–2.5 cm DBH.

Sugar maple sapling distribution and morphology were surveyed across watersheds by establishing 84, $15 \text{ m} \times 15 \text{ m}$ (225 m^2) plots. The location of the plots was based on an existing grid system, from which 42 points were randomly selected without replacement across hardwood and mixedwood stands on each watershed (softwood stands were excluded) (Fig. 1). All sugar maple saplings that fit the above parameters were tagged and measured for DBH (at 1.3 m), height, basal diameter (at 10 cm), and canopy cover.

2.3. Canopy cover assessment

Canopy cover was assessed for each sapling and for each plot using hemispheric canopy photographs, which have been shown to

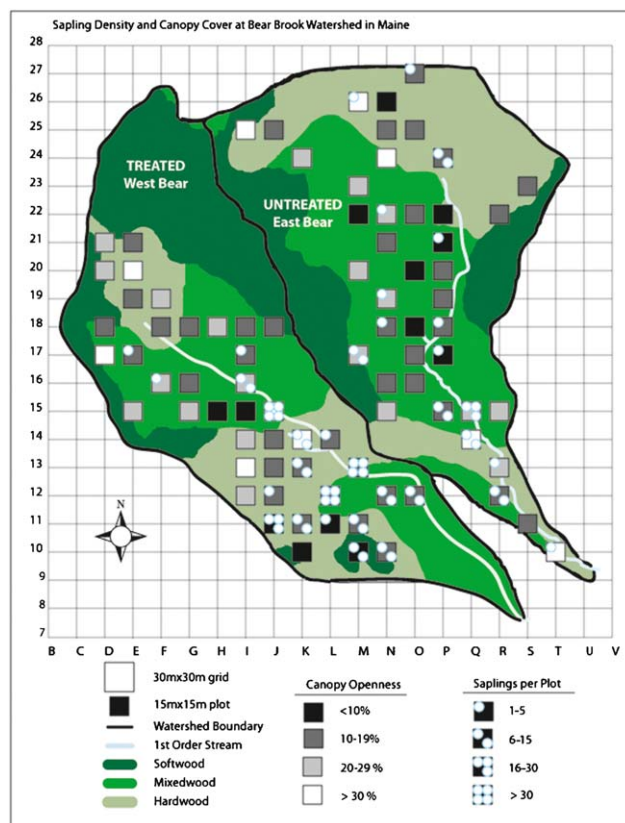


Fig. 1. Map of Bear Brook Watershed Maine showing plot locations, sapling density and canopy cover within plots. West Bear (treated) on the left, East Bear (untreated) on the right.

be one of the best predictors of growth in northern hardwood saplings (Kobe and Hogarth, 2007). Images were taken using a high resolution digital camera with a 180° fish eye lens above the leader of each sapling. Canopy photos were taken on cloudy days in order to avoid sun spots and leaf wash out created by sun glare. Photos were analyzed using Gap Light Analysis Version 2 (Frazer et al., 1999). To optimize the boundary between canopy and sky, a pixel intensity threshold of 190 was used to convert the photographs into a black and white bitmap (Frazer et al., 1999).

2.4. Tree selection

Out of the 84 plots surveyed, 49 of the plots did not contain target saplings. These plots were excluded from further measurements. The target saplings in the remaining 35 plots on both watersheds were used as the sapling population for nutrient, biomass, and physiological measurements.

2.5. Foliar analyses

Three to four saplings per plot (36 and 37 sugar maple saplings from 11 plots from untreated EB and treated WB, respectively) were randomly selected from the population for foliar chemistry analyses. Foliage was sampled and analyzed for C, N, P, K, Ca, Mg, Mn, Al, Fe, Zn, Cu, and B. Leaf blades were collected the second week of August 2006 using powder-free latex gloves and were placed in paper bags. No washing treatment was applied to leaves. Bags were placed in a 70 °C drying room and dried to a constant mass.

Dried leaf blades were ground to a 20 mesh using a Wiley mill. Care was taken to clean the mill between each sample. Chemical analyses were performed at the Analytical Laboratory of the Maine Agricultural and Forest Experiment Station at the University of Maine. Total N was determined by the combustion (Dumas) method. Other elements were determined by inductively coupled plasma atomic emission spectrophotometry (ICP-AES) following dry ashing at 550 °C for 5 h in a muffle furnace with dissolution in 50% HCl (Kalra and Maynard, 1991).

2.6. Photosynthetic rates and capacity

Fifteen saplings (three saplings per plot) per watershed that occurred in small gaps in five plots where canopy openness was between 12 and 25% (Beaudet et al., 2000) were randomly selected for physiological analyses which included A–C_i curves, foliar chemistry and LMA (leaf mass per area). Photosynthetic capacity was measured in a three-week period in late July and early August on saplings using a LI-6400 gas exchange system (Li-Cor, 1998) to produce A–C_i curves (Farquhar et al., 1980).

The three main components to photosynthesis were measured: (1) carbon fixation by rubisco, (2) electron transport from light harvesting chlorophyll, and (3) tri-phosphate exchange with inorganic phosphate (Sharkey, 1985). A–C_i curves provided estimations of (1) maximum carboxylation capacity (V_{cmax}), (2) maximum electron transport (J_{max}), and (3) triose-phosphate utilization (TPU), using the Nelder–Mead simplex method (Photosynthesis Assistant Software, Dundee Scientific, Scotland, UK) based on parameters developed by Harley et al. (1992).

Measurements were conducted at the leaf-level in the upper canopy of each sapling that had recent exposure to sunlight. Within the leaf chamber, leaves were exposed to a saturating irradiance of 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ using a red/blue LED light source (Beaudet et al., 2000). Leaf temperatures were held close to ambient (20–26 °C). Measurements were taken when conditions within the cuvette were stabilized below a total coefficient of

variation of 0.3. Vapor pressure deficit (VPD) was kept below 1.5 MPa.

Leaves were collected for leaf mass area (LMA, g m^{-2}) measurements from the same saplings measured for photosynthetic parameters. In the lab, leaf area was measured on an LI-3100 with 11 moist leaves per sapling.

2.7. Sapling growth and above ground biomass

Fifteen saplings (3 saplings from each physiology plot) were selected near the end of the growing season for dendrochronology and aboveground biomass analyses. Each tree was cut at ground level and all leaves and woody materials were collected. The bole was measured and cut into 0.3 m increments. Trees were dried in a 70 °C drying room and each component (bole, leaves, and branches) was weighed to calculate aboveground biomass.

Sections of bole wood were sampled for growth analysis. Discs were cut from the base of the bole, at 0.3 m, and every subsequent 0.6 m section until the leader was reached. Discs were sanded to an 800 grit, and zinc oxide was used to bring out the rings more clearly. The discs were scanned to 1600 dpi on a flatbed scanner. Tree rings were measured on four to eight discs per tree, depending on the length of the bole. Annual ring widths were counted and measured to the nearest 0.001 mm with a tree ring increment measurement system (WinDendro v6; Regent Instruments, Université du Québec a Chicoutimi, Québec). Each disc had two radii of analyses, avoiding tension wood. Each radius was analyzed twice and compared in order to minimize error.

Tree ring data from each height were pooled for each tree and annual height and volume growth were calculated using WinStem (Regent Instruments, Université du Québec a Chicoutimi, Québec). Height curves were interpolated using the Carmean method (Carmean, 1972; Dyer and Bailey, 1987).

2.8. Statistical analysis

Statistical analyses were conducted using SYSTAT v.12 [SPSS Science, Chicago, Illinois]. Two sample *t*-tests were used to analyze each set of data for significant differences by watershed. Log transformations were used, as specified in data tables, to meet normal distribution assumptions. Treatment differences were considered significant at $\alpha < 0.05$. Using the combined data from both watersheds, Pearson correlations and linear regressions were performed to assess relationships between nutrients, growth rates, and photosynthetic capacity.

3. Results

3.1. Sapling demography and watershed canopy cover

Sugar maple sapling density averaged 81 saplings per hectare on untreated EB and 358 per hectare on treated WB. The highest number of saplings per plot on the untreated EB was 16 while the maximum plot density on the treated WB was 119. Using only plots with saplings, both *t*-tests and the Mann–Whitney test (for highly skewed data) showed no statistical differences in sapling density across treatments ($p = 0.287$).

Hemispheric photography showed no significant differences in canopy openness, 17.9 and 18.6% in untreated EB and treated WB, respectively (Table 1). Photographs taken above the leader of each sapling showed similar light environments for saplings across treatments with 12.3 and 12.0% openness in untreated EB and treated WB, respectively. Regressions between sapling density and canopy cover showed non-significant relationships ($R^2 = 0.0017$, $p = 0.72$).

Table 1

Mensurational data from the 2 to 4 m size class sugar maple saplings. Means based on 84 plots and 422 saplings. SE: standard error.

	East Bear – untreated, mean (SE)	West Bear – treated, mean (SE)	<i>t</i> -tests, <i>p</i> -values
Saplings per plot	1.8 (0.5)	8.0 (3.3)	0.09 ^a
Saplings per ha	81 (24)	358 (146)	0.08
Sapling Ht (m)	2.6 (0.02)	2.6 (0.03)	0.55
Sapling DBH (mm)	10.6 (0.2)	10.5 (0.2)	0.95
Sapling basal diameter (mm)	17.8 (0.2)	17.0 (0.3)	0.22
Plot canopy openness (%)	17.9 (1.5)	18.6 (1.3)	0.55 ^a
Sapling canopy openness (%)	12.3 (0.5)	12.0 (0.4)	0.76

^a Based on log transformation.

Table 2

Foliar nutrient concentrations for sugar maple saplings. Untreated *n* = 36; treated *n* = 37. C and N are percent by mass, other nutrients are in parts per million (ppm). SE: standard error.

Element	East Bear – untreated, mean (SE)	West Bear – treated, mean (SE)	<i>t</i> -tests, <i>p</i> -values
C	47.6 (0.1)	47.8 (0.1)	0.272
N	2.03 (0.04)	2.38 (0.03)	<0.001
P	1102 (20)	1230 (27)	<0.001 ^a
K	8274 (291)	9736 (316)	0.001
Ca	6922 (312)	5367 (262)	<0.001 ^a
Mg	1380 (54)	1253 (41)	0.066
Mn	965 (60)	1064 (76)	0.323 ^a
Al	16.9 (1.5)	29.9 (1.5)	<0.001 ^a
Fe	43.1 (1.2)	47.2 (1.0)	0.008 ^a
B	42.9 (1.4)	47.3 (1.9)	0.066
Cu	6.0 (0.2)	6.1 (0.2)	0.726
Zn	23.8 (1.6)	23.5 (0.7)	0.574 ^a

^a Based on log transformation of the data.

3.2. Foliar chemistry

Foliar chemistry of saplings showed several strong differences between saplings from treated and untreated watersheds. Nitrogen, P and K concentrations were significantly higher in treated saplings compared to untreated saplings (Table 2). Al was 56% higher in treated sapling foliage, while Ca was 25% lower (Fig. 2). Foliar Mg concentrations were lower on treated sapling foliage but these differences were not significant despite a significant positive correlation between Ca and Mg foliar concentrations ($r = 0.66$, $p < 0.001$). There was a numerical trend for higher trace metal concentrations in treated foliage, but only Fe concentrations were significantly greater.

Stoichiometric relationships among elements also suggested important differences between treated and untreated saplings. C:N and Ca:Al ratios were significantly lower for treated saplings compared to untreated saplings (Table 3). Conversely, N:P ratios

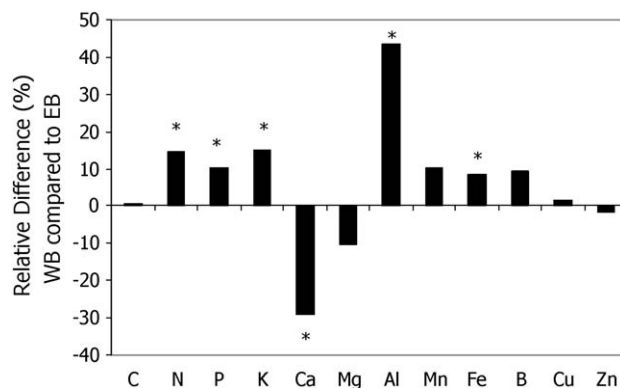


Fig. 2. Differences in foliar nutrients between treated and untreated sugar maple saplings (e.g. Ca is 25% lower on treated compared to untreated). Untreated *n* = 36; treated *n* = 37. * indicates significance at $\alpha = 0.05$.

Table 3

Foliar stoichiometry of sugar maple saplings. Untreated *n* = 36; treated *n* = 37. Ca:Al ratios are based on molar concentrations, other ratios are based on mass concentrations.

	East Bear – untreated, mean (SE)	West Bear – treated, mean (SE)	<i>t</i> -tests, <i>p</i> -values
C:N	23.8 (0.1)	20.2 (0.2)	<0.001 ^a
N:P	18.5 (0.2)	19.6 (0.3)	<0.001
Ca:Al	451 (66)	136 (11)	<0.001 ^a

^a Based on log transformation data

were significantly higher in treated saplings, largely driven by higher nitrogen levels.

3.3. Components of photosynthesis

The A–C_i curves of treated saplings were highly variable in response to increasing levels of CO₂, while untreated saplings had more uniform A–C_i curves (Fig. 3).

Untreated saplings showed greater overall photosynthetic capacity than treated saplings (Table 4) with mean levels of $V_{C_{max}}$, J_{max} , and TPU lower in treated saplings. Respiration was also lower on the treated saplings. There were no significant differences in conductance or light-saturated net photosynthesis (A_{net}) at 400 ppm (near ambient) CO₂. Leaf mass area was similar between treatments, averaging 31.8 and 32.1 g m⁻² in untreated and treated saplings, respectively.

Both environmental variables and nutrient concentrations were correlated with photosynthetic capacity (Table 5). Mean leaf temperature (23.8 °C) was significantly higher in untreated saplings than treated saplings (21.4 °C) and was positively correlated with $V_{C_{max}}$, J_{max} , and TPU. Sapling density (saplings per plot) was negatively correlated with all components of

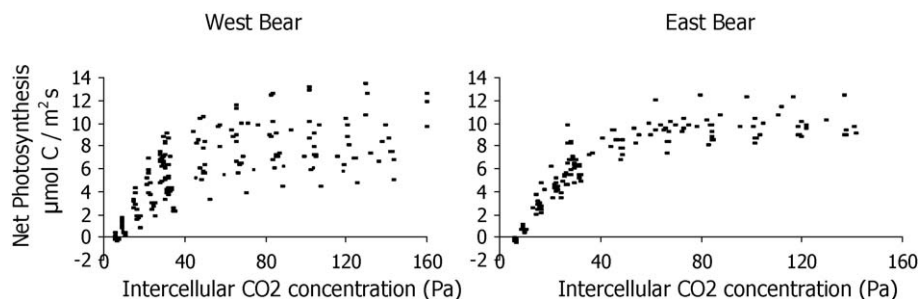


Fig. 3. Individual A–C_i curves of sugar maple saplings at the BBWM. Untreated *n* = 12; treated *n* = 14.

Table 4

Photosynthetic parameters for Bear Brook sugar maple saplings. Untreated $n = 12$; treated $n = 14$. V_{cmax} : carboxylation capacity, J_{max} : electron transport capacity, TPU: triose-phosphate utilization, A_{net} : light-saturated net photosynthesis, Resp: respiration, Cond: stomatal conductivity to CO_2 , LMA: leaf mass per area. Units are $\mu mol\ m^{-2}\ s^{-1}$, except LMA $g\ m^{-2}$ and Cond that are $mol\ m^{-2}$. * indicates significance.

	East Bear – untreated, mean (SE)	West Bear – treated, mean (SE)	t-test, p-values
V_{cmax}	19.40 (1.03)	14.73 (1.26)	0.010*
J_{max}	50.38 (1.92)	42.98 (2.58)	0.035*
TPU	3.54 (0.10)	3.08 (0.18)	0.044*
A_{net}	5.82 (0.29)	5.79 (0.50)	0.956
Resp	1.12 (0.05)	0.94 (0.06)	0.044*
Cond	0.10 (0.03)	0.10 (0.03)	0.534
LMA	31.8 (0.86)	32.1 (0.62)	0.696

Table 5

Significant regression coefficients from Pearson correlations of photosynthetic parameters. Data from both watersheds combined ($n = 24$). “ns” indicates no significant regression for those variables. Sapling ht, DBH, K, Mg, B, and Cu were also correlated with photosynthetic parameters, but there were no correlations with a p-value less than 0.1. See Tables 1, 2 and 4 for units.

Regression variable	Photosynthetic parameters			
	V_{cmax}	J_{max}	TPU	A_{net}
N	ns	−0.364*	ns	ns
Ca	0.396*	ns	ns	ns
Al	−0.430**	ns	ns	ns
P	ns	−0.492**	−0.498**	ns
Mn	ns	−0.614***	−0.693***	ns
Zn	ns	−0.585***	−0.477**	ns
Fe	−0.471**	−0.511**	−0.469**	ns
Sapling density	−0.495**	−0.436**	−0.377*	−0.374*
Leaf temperatures	0.754***	0.472**	0.430**	ns
Canopy openness	0.403*	ns	ns	ns

* $p < 0.1$.

** $p < 0.05$.

*** $p < 0.01$.

photosynthetic capacity, including A_{net} . In turn, leaf temperatures were negatively correlated with sapling density ($R^2 = 0.505$, $p = 0.0001$). Canopy openness was weakly positively correlated with V_{cmax} .

Nutrients closely associate with sugar maple decline showed some correlation with photosynthetic capacity. J_{max} had a weak negative correlation with leaf N concentrations. Ca showed a weak positive correlation with V_{cmax} , while Al showed a significant negative correlation with V_{cmax} . Mn and P also showed a significant negative correlation with J_{max} and TPU. Fe and Zn, micronutrients not commonly associated with sugar maple decline, showed a significant negative correlation with J_{max} and TPU. Fe was also negatively correlated with V_{cmax} .

3.4. Sapling biomass and growth

The average age was 17 for treated saplings and 19 for untreated saplings, which puts the majority of their life span within the period of the treatment. Positive correlations between height and DBH were strong in both watersheds ($R^2 = 0.63$, $p < 0.001$), and the means of sapling height, DBH, and basal diameter were nearly identical across treatments (Table 1). This may reflect the narrow parameters used in sapling selection. Although treated saplings were slightly larger, analyses of above-ground biomass show non-significant differences between watersheds (Table 6). However, untreated saplings had a significantly greater proportional allocation to foliar biomass, while treated saplings allocated more biomass to stem growth.

Table 6

Sapling age and growth rates based on stem analysis. * indicate significance.

	East Bear – untreated, mean (SE)	West Bear – treated, mean (SE)	t-test, p-values
Age	19.1 (0.8)	17.0 (1.0)	0.089
Growth/year (g)	13.7 (2.2)	19.5 (3.2)	0.184 ^a
Avg ann vol growth (cm^3)	8.4 (1.7)	12.4 (2.3)	0.252 ^a
Avg of last 5 yr vol growth (cm^3)	21.8 (4.7)	30.2 (5.4)	0.163 ^a
Avg ht growth (cm)	14.4 (1.1)	18.4 (1.6)	0.048 ^a
Avg of last 5 yr ht growth (cm)	21.3 (2.0)	26.5 (2.2)	0.096

^a Log transformed.

Table 7

Aboveground biomass for Bear Brook sugar maple saplings. Untreated $n = 15$; treated $n = 15$.

	East Bear – untreated, mean (SE)	West Bear – treated, mean (SE)	t-test, p-values
Aboveground biomass (g)	265 (43)	338 (67)	0.397 ^a
Leaf biomass (g)	41.7 (5.1)	40.1 (7.0)	0.850
Woody biomass (g)	213 (39)	298 (60)	0.282 ^a
Fraction in leaves (%)	17.6 (0.01)	12.8 (0.01)	0.005
Fraction in wood (%)	82.0 (0.01)	87.2 (0.01)	0.005

^a Based on log transformation data.

Stem analysis showed that saplings in the two watersheds were of similar age and had experienced similar stem volume growth (Table 7). Height growth showed significantly higher growth rates on the treated watershed, particularly due to greater than average growth during the years 1997 and 1998. Height growth in the past five years shows a gradual return to similar rates of growth between treatments.

4. Discussion

4.1. Sapling distribution and growth

Though there were a number of highly concentrated populations of sugar maple saplings on both watersheds, there were no statistically significant differences in sapling demographics between the treatments. Our results suggest that sapling population frequency and density was principally controlled by factors other than N and/or S fertilization. Variations in sapling density are commonly dependent on edaphic conditions, seed rain, seedling establishment, and canopy structure (Walters and Reich, 1996; Catovsky and Bazzaz, 2002; Cole and Lorimer, 2005). Past research indicates the watersheds have had a comparable population of sugar maple mature trees for seed sources (Elvir, 2004) and seedling banks (Kenlan, 2006), although Eckhoff (2000) showed a higher level of seedlings and seed rain on the treated watershed in 1997.

Our results suggest that the dominant factor in Bear Brook sugar maple sapling growth is related to canopy openness resulting from disturbance. Although current canopy openness above the studied sugar maple sapling clusters is similar between watersheds, past growth patterns indicate that superior height growth in the treated watershed is principally the result of canopy disturbance related to ice storm events, particularly a severe storm in the winter of 1997–1998. This storm damaged approximately 11 million acres in Maine (Ireland, 1998). Canopy damage was most severe in hardwood stands, and researchers at the site observed that the treated watershed sustained more damage than the untreated watershed. These events coincided with the large increase in

height growth noted in treated saplings. A similar growth increase has also been documented in subcanopy sugar maple trees following the 1998 ice storm at Hubbard Brook Experimental Forest (Huggett et al., 2007). This growth was likely stimulated by both higher incident light levels increasing carbon gain (Catovsky and Bazzaz, 2002) and a shift in light quality from increased red:far-red light ratios within the understory (Gilbert et al., 2001). Past studies recorded height growths between 20 and 30 cm yr⁻¹ from single tree fall events (Canham, 1985), approximately the average height growth demonstrated by the treated saplings in the late 1990s.

Investigations of morphology, aboveground biomass, and growth also did not demonstrate a clear response to N and S treatment. In mature sugar maple trees there was a significant increase in basal area increment growth in response to nitrogen treatment, which continued for approximately eight years after treatment began and then declined (Elvir et al., 2003). Mature sugar maples on the untreated watershed have seen moderate declines in growth since the early 1990s. Again, suggesting that sapling sugar maples respond differently than mature trees to fertilization and to different external environmental factors.

4.2. Foliar chemistry

Sapling foliar chemistry was clearly suggestive of effects associated with the N and S addition and soil acidification. As expected, N was elevated in treated saplings. Foliar chemistry analyses of all species studied to date on the treated watershed have had higher concentrations of foliar N than on the reference watershed (White et al., 1999; Elvir et al., 2005, 2006; Kenlan, 2006). In this study, higher levels of P and K were also found in the foliage of treated saplings. Seedlings at the BBWM also demonstrated higher levels of foliar N, P, and K concentrations in treated foliage (Kenlan, 2006). Boggs et al. (2005) noted increases in N, P, and K of sugar maples in the early stages of N saturation, which stimulated a fertilization effect. However, this study found no correlations between growth and major foliar nutrients, with sapling growth apparently principally controlled by canopy conditions.

The C:N ratios of sapling foliage on both watersheds were comparable to other N enriched sites. Gradowski and Thomas (2006) found that growth was positively correlated with available P, while Vitousek et al. (1995) found that foliar N and P is often highly correlated in foliage across ecosystems. Tessier and Raynal (2003) suggested that N:P ratios above 16 were indicative of possible N saturation and P limitations. At the BBWM, foliar N:P ratios were above that threshold and were higher in treated saplings than in untreated saplings, due to a greater increase in foliar N than foliar P concentrations. This result may suggest that P uptake is not keeping pace with N uptake, though we see no evidence that this is impacting growth.

Foliar Ca:Al molar ratios have been both supported (Cronan and Grigal, 1995; Schaberg, 2006) and refuted (Boggs et al., 2005) as good indicators of acidification and decline in sugar maple. Long (1997) suggested a threshold below 110 or less may be associated with sugar maple decline. Treated saplings on West Bear have surpassed this threshold with an average molar Ca:Al ratio of 136. Calcium and Mg are considered elements of concern for sugar maple across the northeast United States. Calcium and Mg foliar concentrations below 5000 ppm and 1100 ppm, respectively, are considered deficient for sugar maple (Kolb and McCormick, 1993). Treated saplings on West Bear were near that level at 5400 ppm. Magnesium, which often declines in conjunction with Ca being very similar geochemically, was also approaching critical levels. Manganese, which may have had a negative effect on respiration, electron transport, and triose-phosphate utilization, were at half

the levels of declining sites in Pennsylvania, where Mn has been considered at toxic levels for sugar maple (St Clair and Lynch, 2005b; Kogelmann and Sharpe, 2006).

4.3. Physiology

Average light-saturated net photosynthesis was 5.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ across both watersheds and showed a weak correlation with sapling density and no significant correlations with any foliar element. A_{net} measured in codominant canopy-level sugar maple was higher than in the saplings, which is expected considering the differences in light environment and sun-shade foliar adaptation (Elvir et al., 2006). Elvir et al. (2006) found significantly higher levels of photosynthesis in the treated watershed (7.3 and 8.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on untreated and treated, respectively), which was associated to higher levels of foliar N. Conversely, foliar N was negatively associated with J_{max} in saplings.

Photosynthetic carboxylation capacity (V_{cmax}) and electron transport (J_{max}) were higher in the untreated saplings, which indicate a greater underlying photosynthetic capacity in untreated saplings. Our findings are in contrast with the commonly accepted positive relationship between nitrogen content and photosynthetic capacity (Evans, 1989), and with the photosynthesis-N relationship reported for overstory sugar maple (Elvir et al., 2006).

The lower photosynthetic capacity and high N:P ratios for treated saplings as well as the negative correlation between leaf N and J_{max} , may indicate nutrient imbalances at the sapling level. The negative correlations of both N and P with photosynthetic capacity are not likely related to their direct effects on photosynthesis (as the literature clearly demonstrates positive relationships). Rather, it is more likely related to the nutrient imbalances demonstrated in the foliar nutrient analyses and potential metal toxicity. For example, TPU, a process highly dependent on P, is most likely related to the rates of cycling in the triose-phosphate and inorganic phosphate pools. This cycling is dependent on trace metals, such as Fe, Mn, and Zn, for electron transport and the building of ATP (Raven et al., 1999).

Our correlation analysis suggests that the high levels of Mn and Zn might have negatively influenced electron transport and triose-phosphate utilization, though foliar Mn was not at levels that are considered toxic in the literature (Kolb and McCormick, 1993). St Clair and Lynch (2005b) found that high inputs of Mn can reduce electron transport rates, as well as reduce sugar maple seedling biomass, but at three times the Mn levels seen in BBWM saplings. The results of this study may show negative effects of higher levels of Mn on J_{max} and TPU that are not apparent when net photosynthesis or growth parameters are considered. The lack of effects at the A_{net} and whole-plant growth scales may be due to the overwhelming influence of light environment on these parameters. Although Zn was significantly related to depression of electron transport and TPU, its potentially toxic effects on sugar maple have not been studied. The positive relationship of Ca and negative relationship of Al to carboxylation capacity also is indicative of nutrient imbalance and is supportive of the hypothesis that calcium may be at critically low levels in these saplings.

Photosynthetic capacity appears to be strongly correlated with the influence of sapling density on energy environments. V_{cmax} , J_{max} , and TPU were significantly correlated with leaf temperature, which in turn was correlated with sapling density. This may indicate that increased foliar temperatures are a result of an enhanced radiation environment at the level of the individual leaf. Interestingly, air temperatures did not correlate with leaf temperature or photosynthetic capacity, suggesting that density has a greater influence on leaf temperatures in the understory than bulk air temperatures.

Untreated saplings showed the greatest allocation of resources to leaf biomass and leaf area, and a lower allocation to stem biomass and height growth. Though the mean canopy openness (measured above the individual saplings) is not significantly different between treated and untreated saplings, there is a weak positive correlation between $V_{C_{max}}$ and canopy openness, suggesting that, the untreated saplings may also be in a slightly better light environment. In addition, our methods of hemispheric photography and photoanalysis cannot determine the relative distribution of canopy gaps into large and small diameters and proximity to saplings. In the latter case, the relative light intensity experienced by the saplings will be determined by the numbral/prenumbral effects of gap diameter and height (Smith et al., 1989). Light quality (red:far-red wavelengths) may vary due to topography, canopy structure, and overstory species differences. These differences in light quality can, in turn, influence resource allocation and relative height growth in saplings (Gilbert et al., 2001).

5. Conclusions

Long-term acidification treatment with $(\text{NH}_4)_2\text{SO}_4$ has resulted in significant increases of foliar N, Al, P, K and significant decreases in foliar Ca in sugar maple saplings. Lower photosynthetic capacity, high N:P ratios, and negative correlation between leaf N and J_{max} , may indicate nutrient imbalance at the sapling level.

There is also evidence that carboxylation capacity has been reduced by foliar nutrient imbalances linked to low Ca and high Al. Other components of photosynthetic capacity, particularly electron transport efficiency and triose-phosphate utilization, appear negatively influenced by increased foliar Mn, Fe, and Zn content, although the levels found in this study are below those that provide obvious symptoms of toxicity.

Photosynthetic capacity also appeared to be closely linked to sapling density which altered light environment at the leaf-level and increased foliar temperatures. Light-saturated net photosynthesis and sapling growth were not correlated with differences in foliar nutrient content. Sapling stratum growth and allocation appeared to be determined primarily by disturbances in the overstory canopy that enhanced light conditions in the sapling stratum.

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